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Abundance and distribution of the white shark in the Mediterranean Sea

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Abstract

Conservation of apex predators is a key challenge both in marine and terrestrial ecosystems. The white shark is a rare but persistent inhabitant of the Mediterranean Sea and it is currently assessed as "critically endangered" in the region. However, the population trends and dynamics of this species in the area are still unknown. Little is known about white shark distribution, habitat use and population abundance trends, aspects that are critical for conservation and management. In this study, we built the most comprehensive database of white shark occurrence records in the region. We collected 773 different records from different sources and used them to characterize the spatial and temporal patterns of abundance of Mediterranean white sharks between 1860 and 2016. We analysed these data by using generalized additive models and used spatially disaggregated information on human population abundance as a proxy of observation effort. Our results suggest a complex trajectory of population change characterized by a historical increase and a more recent reduction (61%, range 58%–72%) since the second half of the 20th century. In particular, analyses reveal a 52% (range 37%–88%) to 96% (range 92%–100%) overall decline in different Mediterranean sectors and a contraction in spatial distribution. Here, we provide the first reconstruction of abundance trends and offer new hypotheses regarding the drivers of change of white sharks in the Mediterranean. Our approach can be broadly applied to data-poor contexts to reconstruct change and inform the conservation of endangered top predators in the Mediterranean Sea and other intensely used marine regions.

KEYWORDS

Mediterranean Sea, observation effort, opportunistic and sparse data, spatio-temporal patterns, standardized trends, white shark

1 | INTRODUCTION

The loss of top predators is one of the most challenging forms of global environmental change, with still unrecognized and not well-understood ecosystem effects (Estes et al., 2011). The decline of large predators on land started approximately 50 kya with the great demographic and geographic human expansion (Dirzo et al., 2014; Ripple et al., 2014). In the oceans, recent increases in resource exploitation by high seas industrial fishers as well as artisanal fleets, habitat degradation and climate change pose unprecedented challenges also to marine predators (Worm & Tittensor, 2011). In the Mediterranean Sea, predator loss is more severe than other ocean sectors due to thousands of years of human impact on marine communities (Coll et al., 2010) and currently high cumulative human pressure on marine ecosystems (Micheli et al., 2013). However, it is only in the last 50 years that systematic data started to be gathered to evaluate the impact of fishing on exploited marine populations and ecosystems (Ferretti, Jorgensen, Chapple, Leo, & Micheli, 2015; McClenachan, Ferretti, & Baum, 2012). This lack of historical baselines hampers our ability to fully understand the ecology of habitats and species, and consequently, our ability to evaluate the conservation status of Mediterranean ecosystems and marine populations.

Among marine animals, sharks are one of the marine taxa with the highest percentage of threatened species (Dulvy et al., 2014). They are generally vulnerable animals, with very low resilience and biological productivity, strongly susceptible to fishing pressure (Ferretti, Worm, Britten, Heithaus, & Lotze, 2010; Queiroz et al., 2019), though examples of sustainable shark fishery also exist (see for details Simpfendorfer & Dulvy, 2017). Because of these features, in the past decades, many shark populations showed rapid declines in multiple marine regions mostly because of the direct effect of targeted and bycatch fisheries (Baum & Blanchard, 2010). An among global ocean sectors, the Mediterranean Sea showed the worst population declines and conservation statuses for many populations (Cavanagh & Gibson, 2007; Ferretti, Myers, Serena, & Lotze, 2008). In 2016, the International Union for Conservation of Nature (IUCN) compiled the second regional assessment of sharks and rays in the Mediterranean Sea, reporting that after ten years the situation had not improved and the conservation status of these species remained probably the worst in the world (Dulvy, Allen, Ralph, & Walls, 2016). In fact, 39 of the 73 assessed species are still threatened and 13 are still considered Data Deficient (Dulvy et al., 2016). Moreover, for most non-data-deficient species, the risk assessment was based on suspected trends and not adequately supported by quantitative analyses. For instance, the conservation status of the white shark (*Carcharodon carcharias*, Lamnidae) was raised from Endangered to Critically Endangered in both Mediterranean and European Regional Red Lists (Dulvy et al., 2016; Nieto et al., 2015) solely on the ground of its current sporadic occurrence in the region and suspected declines.

The white shark is one of the largest and most widespread top predators in the ocean. It is broadly distributed between the subpolar and subtropics in both hemispheres, with major coastal aggregation sites in temperate latitudes (Compagno, 2001). Most of the biological and ecological research on white sharks have been carried out in three coastal aggregation sites (Huveneers et al., 2018): California (Chapple et al., 2011; Tinker, Hatfield, Harris, & Ames, 2016), southern Australia (Bruce & Bradford, 2012) and South Africa (Kock et al., 2013). Here, satellite and acoustic tagging, genetics and isotopes analyses have deepened our ecological understanding of the species' migrations, preferred habitats, population structure, abundance and distribution patterns (Bruce & Bradford, 2012; Carlisle et al., 2012). Even if a general assessment of the white shark abundance trends is challenging to achieve, there have been several attempts in different areas to assess the status of the sharks. Locally, different data sources and modelling approaches have been adopted (Christiansen et al., 2014; Curtis et al., 2014; Dudley & Simpfendorfer, 2006; Lowe et al., 2012; Reid, Robbins, & Peddemors, 2011). Most of these attempts showed a slow increase in white shark populations or subpopulations relative abundance in recent years due to the presence of local protecting measures (Curtis et al., 2014; Dudley & Simpfendorfer, 2006; Lowe et al., 2012; Reid et al., 2011). By contrast, relative declines have been detected in regions lacking these measures (Christiansen et al., 2014). Despite both the protecting provisions existing and the actual conservation status, no white shark population trend analyses have been carried out in the Mediterranean basin, so far.

In the Mediterranean Sea, white sharks have been sporadically but regularly detected throughout history. Several authors (Fergusson, 1996; Gubili et al., 2011) hypothesized the existence of a distinct Mediterranean population, and phylogeographic analyses showed a large genetic distance and scarce genetic flow between the Mediterranean and north-western Atlantic white sharks (Gubili et al., 2011, 2015). However, little is known about the ecology and biology of the Mediterranean population. Studying white sharks in the Mediterranean Sea is challenging because of the low population density and the absence of conventional aggregation sites, such as around pinnipeds colonies (Klimley & Anderson, 1996). This makes it challenging to conduct monitoring studies with the use of electronic tagging, and limits the scope of genetic and isotopic analyses (Gubili et al., 2011). However, opportunistic occurrence records exist (Boldrocchi et al., 2017; De Maddalena & Heim, 2012; Fergusson, 1996; Serena, Mancusi, & Barone, 2008). Regional reviews of these data generated interesting hypotheses on patterns in population structure, movements and abundance. For example, several catches of young-of-the-year white sharks reported for the Sicilian Channel suggested the presence of a nursery area in this sector (Fergusson, 1996, 2002). The reduction in white shark sightings through the years from areas with a parallel strong decline of tuna populations, combined with recent and historical sightings in and around farm pens and tuna traps (Galaz & De Maddalena, 2004; Storai et al., 2011), suggested a close relationship between Atlantic Bluefin tuna (*Thunnus thynnus*, Scombridae) and white shark occurrence in the Mediterranean Sea (Boldrocchi et al., 2017; De Maddalena & Heim, 2012; Kabasakal, 2016). Yet, more research is needed to understand population structure, size, movements and distribution within the area and their relations with environmental and biological variables.

Mediterranean white shark observation records are opportunistic because they are often collected from fishers' anecdotes or newspaper articles (Pearce & Boyce, 2006), and, hence, obtained without a specific and systematic sampling effort. Nevertheless, in the absence of systematic surveys, opportunistic data provide valuable insights on species distribution, habitat requirements and population trends (Christiansen et al., 2014; Curtis et al., 2014; Ferretti et al., 2015). For example, McPherson and Myers (2009) used white shark sightings collected between 1868 and 2005 to infer population changes in the Adriatic Sea. They estimated temporal trends of occurrence records under different scenarios of observation effort and estimated an 84% decline (CI: +27% and −98%). These estimates were highly uncertain as the authors had no direct information on observation effort but provided a first quantitative estimate of white shark population change in a sector of the Mediterranean Sea. Here, we expand on this approach to produce the first regional assessment at the Mediterranean scale. We assembled the most comprehensive database of white shark's occurrence records currently available for the Mediterranean Sea and estimated trends controlling for observation effort, which was directly estimated with long-term trend models of coastal human population censuses in the region. We used these standardized records to infer trends in population abundance and asked whether, how and how much the white shark population has changed in abundance and spatial distribution over the last two centuries.

2 | METHODS

2.1 | Shark database construction and exploratory analysis

We built a database containing all the white shark records in the Mediterranean Sea using different sources and multiple search strategies (Supporting Information), also including existing institutional databases, such as MEDLEM (Mediterranean Large Elasmobranchs Monitoring) currently under the auspices of the General Fisheries Commission for the Mediterranean Sea (GFCM, Serena et al., 2008). We followed through citations in the listed references to delineate the history of each account and to determine whether the record was original or redundant (reporting records from other publications) (Ferretti, Morey Verd, Seret, Sulić Šprem, & Micheli, 2016). For each observation we recorded: date and location; total length; weight; sex; age (adapted from Bruce & Bradford, 2012; Supporting Information); record type (stranding, catch, sighting, signs of predation on other marine animals); stomach contents; fishing gear involved in the capture; and bibliographic reference for published accounts. Then, we performed an exploratory data analysis in order to evaluate the most immediate ecological information, such as the sightings' temporal and spatial distribution, length frequency, length–weight relationship and a qualitative stomach content analysis (Supporting Information).

2.2 | Model framework

We stratified the Mediterranean sea in spatio-temporal statistical units of different resolution (e.g. FAO or GFCM statistical sectors and year) and following McPherson and Myers (2009)'s approach, we assumed that the expected number of sightings per statistical unit (year *t* and geographic sector *s*) was related to the following variables: number of possible observers (observation effort), O_{ts}, their propensity to report a sighting, P_{ts}, white sharks population abundance, N_{ts}, and shark detectability, D_{ts}. In systematic and dedicated surveys, these factors can be controlled. Conversely, this information is incomplete for opportunistic data (McPherson & Myers, 2009). In this work, we chose the human population size (H_{ts}) as a proxy of observation effort. Therefore, we treated O_{ts} and P_{ts} as a joint process, essentially assuming that all observers had a constant probability to report a record (McPherson & Myers, 2009) and that the number of observers is proportional to the human population size ($O_{ts} = cH_{ts}$, where *c* is constant). Hence, we assumed that detectability, D_{ts}, has a proportional relationship with abundance ($D_{ts} = kN_{ts}$), assuming, in other words, that a specific amount of observation effort is needed to detect a fixed proportion of the individuals present in the study area (McPherson & Myers, 2009). This represents the simplest possible scenario to infer standardized abundance trends of the shark population. In fact, under these assumptions, the probability of a recorded sighting depends only on H_{ts} and N_{ts}. We tested deviations from such an assumption in the following inferential analysis.

Given that Mediterranean white shark sightings are rare and discrete events, we assumed that the expected number of sharks per statistical unit follows either Poisson or Negative Binomial (NB, in case of overdispersed data) distributions where their means are a function of predictors describing N_{ts} and H_{ts}. However, it is important to note that factors other than H_{ts} can affect the observation effort variability over space and time. For example, the marine area covered by the potential observers and the technological innovations in fisheries and boating may have played a pivotal role in changing the sightings probability (fisheries have expanded in distance from shore and overall range over time; Rousseau, Watson, Blanchard, & Fulton, 2019). So, the sighting probability may have increased during the 20th century, but testing this hypothesis was not possible with the available data. Therefore, since this issue arises when interpreting the frequency of occurrence of many other Mediterranean species, we explored the performance of a single, readily available and systematic proxy of observation effort.

2.3 | Collecting observation effort data

In order to investigate trends in the spatio-temporal distribution of our proxy of observation effort, we divided the Mediterranean coastline into 202 coastal regions, belonging to 23 different countries and retrieved the human population in each coastal region (Supporting Information) (Figure 1a,b). Historical time series of the human population were collected for each coastal region over a time range of 156 years (1860–2016). Multiple sources, such as national census reports or international databases (Eurostat, World Bank), were consulted to rebuild each human population time series (Supporting Information). As not all considered regions had annual census estimates for the whole time period, we interpolated missing years with a regression approach. Annual population size estimates for each region were obtained by fitting GAMs (Wood, 2011) and log-scale regressions to the historical population censuses data. Then, we selected estimates according to the best fitting model in each region (details are in the Supporting Information).

2.4 | Estimating standardized shark sighting trends

In order to identify the spatial and temporal patterns characterizing the sighting data, we considered a time range of 156 years (between 1860 and 2016) and different levels of resolution for spatial strata. We chose 1860 as our initial observation year because earlier sightings were scarce and previous human population data in most Mediterranean countries were unavailable. Observation effort and shark occurrences were spatially aggregated using both the GFCM's Mediterranean Geographic Sub-area stratification (GSAs, http://www.fao.org/gfcm/data/map-geographical-subareas/en/) (Figure 2a) and the coarser FAO Major Fishing Area 37's stratification of eight divisions (http://www.fao.org/gfcm/data/map-geographical-subareas/en/) (Figure 3b). In order to find the best fitting model, we tested multiple model structures (Supporting Information) with various levels of temporal aggregation, functional relationships between response and predictors (e.g. linear or more complex with polynomials and splines) and the two statistical distributions of the response variable (NB and Poisson). GAMs with 1-year time bins resulted as the best model class in terms of AIC, fitting deviance and residuals analysis. Model fits were performed by using the R package mgcv (Wood, 2011). We fitted a GAM with a Negative Binomial Distribution and a log link function to the annual number of shark occurrences recorded in each GSA, using the observation effort (annual number of people for that GSA) as an offset term and the GSAs as spatial sectors (hereby referred as GSA model). The model structure was

$$\log\left(z_{ij}\right) = f(y_i) + [\mathrm{GSA}]_j + \log(H_{ij}) + \varepsilon_{ij} \tag{1}$$

where z_{ij} is the ith observed number of sharks in year y_i (i = 1, …, 156) and GSA j, f is a smooth function estimated using penalized likelihood maximization (with a smooth parameter estimated by Restricted Maximum Likelihood) (Wood, 2011), $[\mathrm{GSA}]_j$ is a factor with 27 levels (j = 1, …, 27), corresponding to the GSAs), log (H_{ij}) is the offset term and ε_{ij} is the error term for ith observation in GSA j, assumed to be normally distributed around 0 and with variance to estimate.

In our modelling exercises, we faced several issues. First, in order to verify the assumption of a linear relationship between the response variable and the offset term, we fitted a parallel model with a spline on the human population abundance and compared the two model's prediction errors through RMSEs (root mean square error, Supporting Information). Second, although we could expect the observation effort to increase with time, we supposed there could be stages in our observation period where sighting effort changed abruptly (i.e. start of ocean use for bathing, interest in marine science, conflicts and epidemics). Therefore, we tested for the effect of these discrete important events dividing our temporal range in bins characterized by different hypothetic sighting effort regimes (Supporting Information). Finally, there was a trade-off between spatial and temporal resolution. Because of the limited number of sightings from specific Mediterranean sectors, the use of a complex spatial stratification, such as the GSA scheme, with a high temporal resolution, allowed us only to detect a common temporal trend throughout the basin and a sector-specific spatial effect on shark's abundance. It was

$$\log(z_{ij}) = f_j(y_i) + [\mathrm{FAODivision}]_j + \log(H_{ij}) + \varepsilon_{ij} \tag{2}$$

where all terms are the same as in the GSA model except for f_j, which here is sector-specific ($[\text{FAO Division}]_j$, with j = 1, …, 8). In this way, we obtained subregional temporal trends, though with a lower spatial resolution. However, this kind of model parametrization assigns the same number of knots to each sub-regional curve via REML (restricted maximum likelihood). In this way, the trajectories estimated for well-represented sectors (with a high number of records) could have leverage on the others with fewer occurrences recorded. Thus, in order to validate the curves obtained with the FAO model and to avoid the presence of artefacts related to the sparse nature of data, we chose to fit, parallelly, a single-sector model for each division (Supporting Information). Finally, we predicted the expected number of sharks in each spatio-temporal model unit considering a fixed amount of observation effort (five million people), in order to standardize the shark abundance trend on easily interpretable values.

2.5 | Testing for spatial range contraction

Given its "Critically Endangered" status, it is expected the species went through a range contraction together with a decline in population abundance (Worm & Tittensor, 2011). To test for this scenario, we aggregated the data in two main periods (1945–1975, 1976–2016) deemed to have the most comparable regimes of observation effort. We excluded from the analysis all the sightings from before 1945 in order to minimize the bias linked to unaccountable variations of the

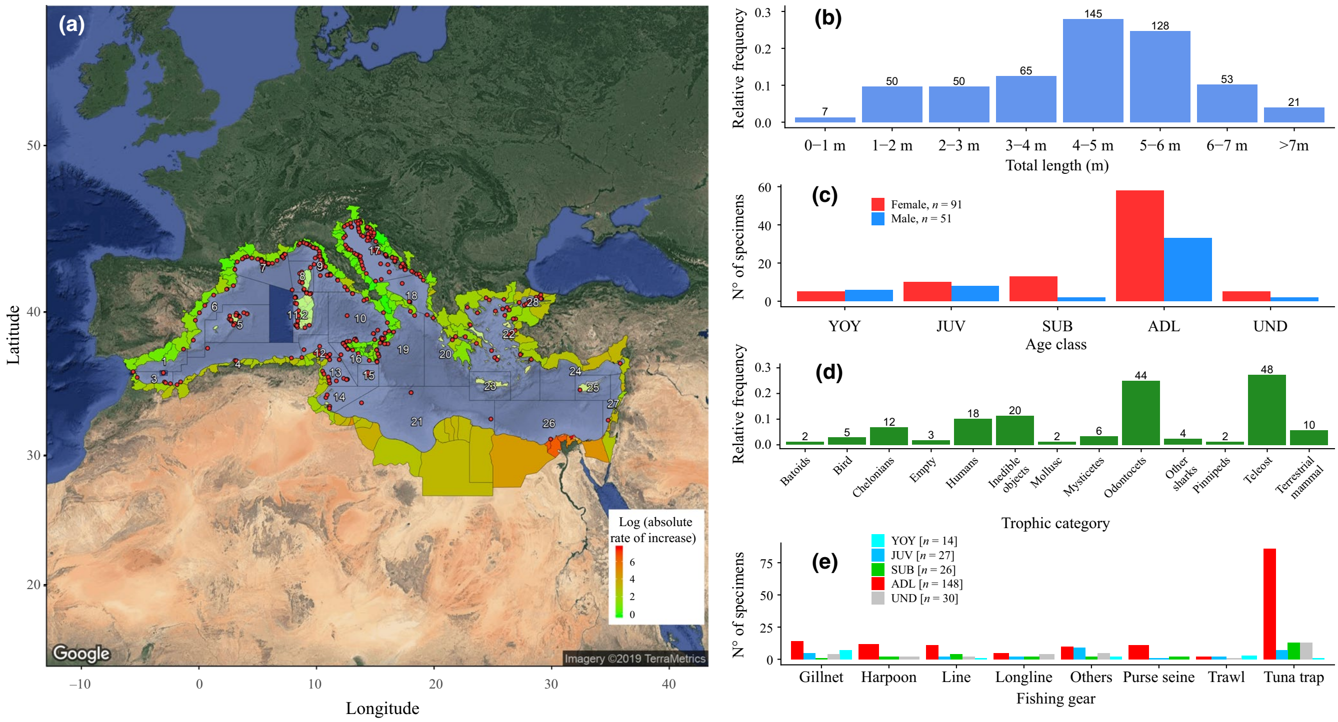

FIGURE 1 Observation effort and exploratory analysis. (a) Absolute variation of coastal regions human population size calculated between 1860 and 2016 and expressed in logarithmic scale. The red dots correspond to the white sharks sighting locations. (b) Length frequency. The absolute frequency is reported over each bar. (c) Sex distribution within age classes (YOY = young-of-the-year, JUV = Juveniles, SUB = Subadults, ADL = Adults, UND = Undetermined). (d) Diet composition. The absolute frequency is reported over each bar. (e) No. of specimens caught by each fishing gear category per age class

observation effort, such as the two World Wars presence. In addition, our aim was to test for a relatively recent decline associated with a spatial range contraction. Hence, we fitted a negative binomial generalized linear model (GLM) (R package MASS, Venables & Ripley, 2002) to the annual number of shark occurrences (considered as replicates) for each time bin in each FAO division, still maintaining the observation effort as an offset term. The model structure was.

$$\log(z_{ij}) = \beta_0 + \beta_1 (T_i) \bullet \beta_2[\text{FAODivision}]_j + \log(H_{ij}) + \varepsilon_{ij} \qquad (3)$$

where z_{ij} is the observed number of sharks in period T_i and FAO division j, β_0 is the intercept, β_{1-2} are regression coefficients, T_i is the time bin, [FAO Division]$_j$ is a factor with eight levels (j = 1, ..., 8, corresponding to the spatial sectors), log (H_{ij}) is the offset term and ε_{ij} is the error term for ith observation in each FAO division j. Hence, we predicted the expected number of sharks in each FAO division for each period considering a fixed value of observation effort (five million people) and compared this index for each sector between the two different time bins.

3 | RESULTS

3.1 | Exploratory data analysis

We identified a total of 773 white shark records within the Mediterranean Sea, spanning from the end of the Middle Ages (1453) to 2016. However, 93% (718) of these occurred after 1860, which is the period when we had the most reliable data and, consequently, was used for our trend analyses. Fisheries catches accounted for 66% of the records, 48% coming from tuna traps, followed by gillnets (23.0%), hand lines (8%), harpoons (6.4%), purse seines (5.6%) and longlines (5.2%) (Figure 1e). The remaining portions came from strandings, sightings, recorded predation events and bites to humans. Records were mainly distributed in the western Mediterranean Sea, in particular, the Northern Adriatic sea (GSA 17, 20.9%), Ligurian and North Tyrrhenian Sea (GSA 9, 13.8%), Southern Sicily (GSA 16, 9.5%) and off the Balearic Islands (GSA 5, 8.5%); and pertained mainly to adults (42.8%), subadults (10.5%) and juveniles (9.6%) (adapted from Bruce & Bradford, 2012) with the majority of individuals of being from 4 to 6 m long (Figure 1b). However, it is important to emphasize that more than a third (32.8%) of records were lacking length information and, consequently, we could not address the age class. Sex ratio was biased towards women (64.1% of the 142 records having sex), and the individuals that had also information on stomach contents (n = 122) suggested that bony fish were the main prey (27.3%), followed by odontocetes (25.0%), scavenging carcasses of other animals (principally farm animals, pets—5.7% and humans—10.2%) and chelonians (6.8%) (Figure 1d).

Coastal human population increased six-fold since 1860, rising from 29.6 million to 183.8 million in 2016, though this increase was geographically heterogeneous (Figure 1a). The highest increases were detected in the eastern basin sectors, with the maximum rise around

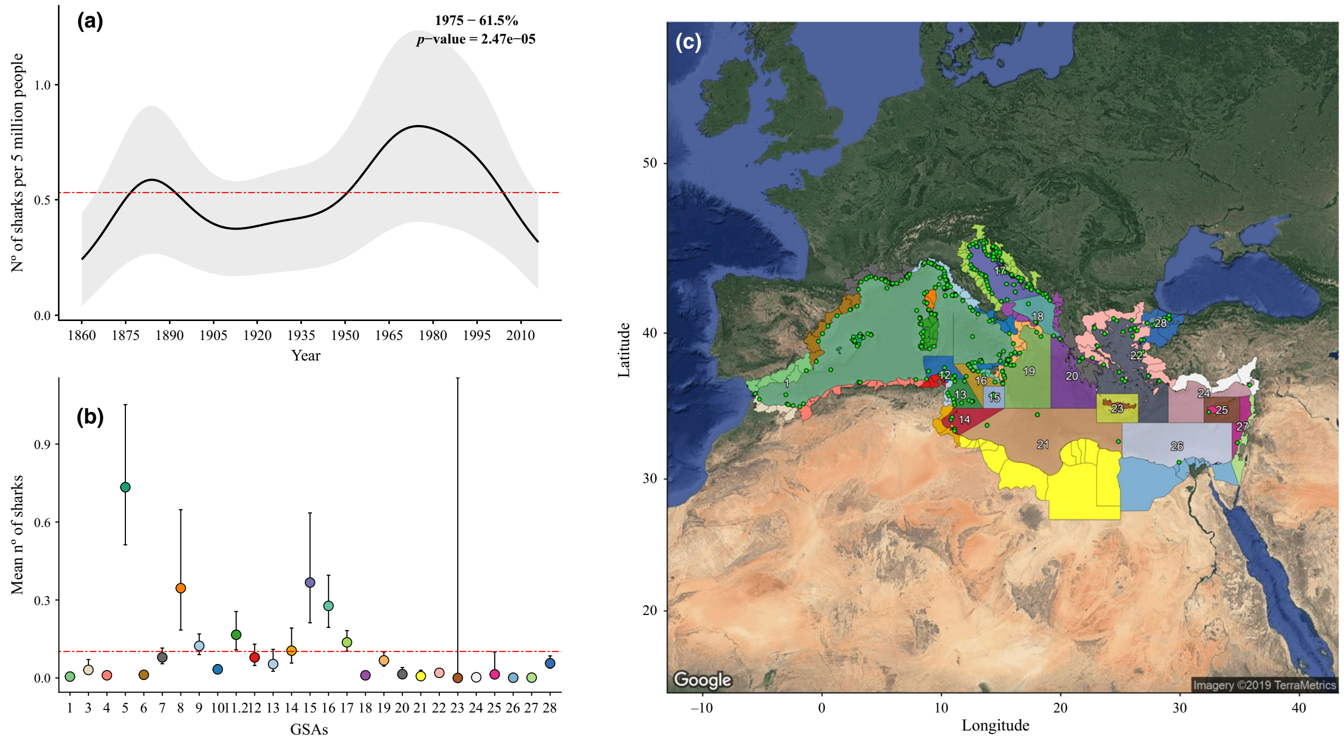

FIGURE 2 Temporal and spatial changes of sighting rate estimated by the GSA model. (a) Temporal effect: expected shark sighting rate between 1860 and 2016 predicted by using a fixed observation effort of five million people. Magnitude of the detected decline, starting year and *p*-value for the smooth term is shown in the top-right corner. The red line is the overall mean sighting rate. (b) Spatial effect: dots are the average variations in mean no. of shark detected in each GSA. Point colour matches colours in the map. Segments indicate the confidence boundaries. (c) Spatial unit used in the model: GFCM Geographic Sub-Areas (as indicated in the Res. GFCM/33/2009/2). The green dots in the map correspond to the white sharks sighting locations extracted from a variety of source observations

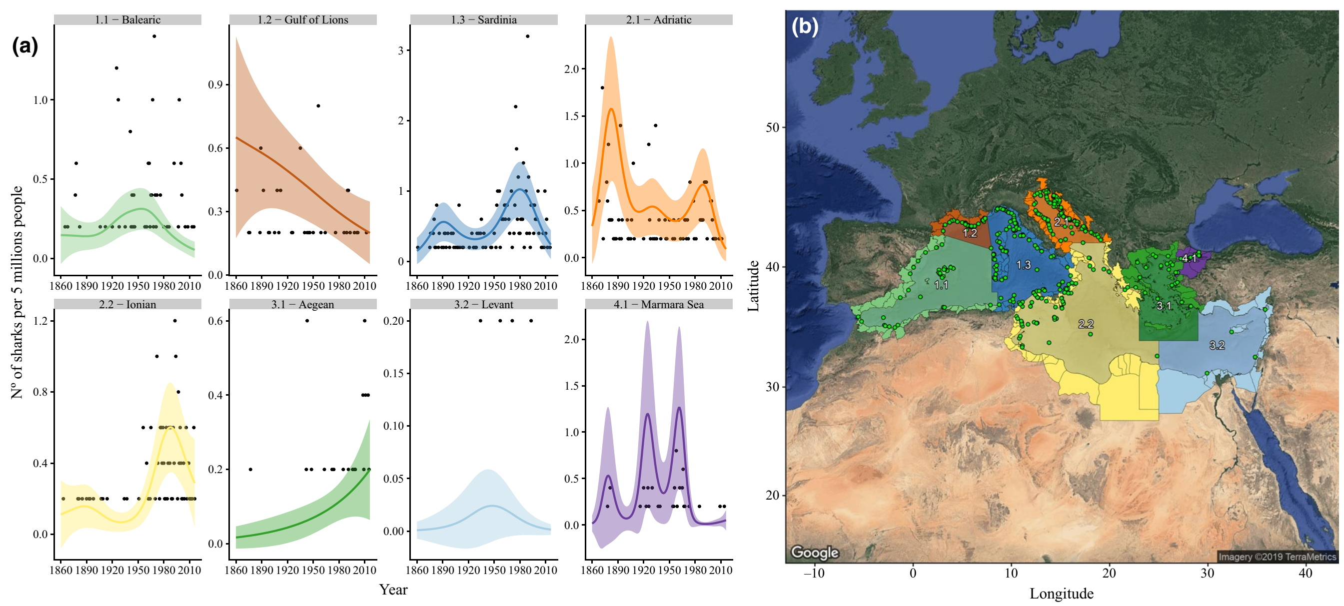

FIGURE 3 FAO model. (a) Mediterranean white shark temporal abundance trend (1860–2016) predicted by the FAO model in each FAO division, considering a fixed observation effort value (five million people). The black dots represent the actual sighting rates (expressed as no. of sightings per five million people) (b) Spatial unit used in the model: FAO Major Fishing Area 37 (Mediterranean and Black Sea) divisions. The green dots in the map correspond to the white sharks sighting locations

the Marmara Sea (319.4-fold). By contrast, the lowest rates of change were observed in the western and central Mediterranean sectors, such as the Northern Adriatic, Southern Sicily and Corsica, where the human population doubled throughout the same period (Figure 1a).

3.2 | Model fitting results

3.2.1 | Temporal trends

Shark observations increased throughout the period (Figure S2), but when we controlled for changes in the potential number of observers (Figure 2a), we detected an initial increase, characterized by two peaks in the 1880s and a higher one in the 1980s, followed by a 61% (range 58%–72%) decline between 1975 and 2016. Similarly, to the changes in the human population, this trajectory was not homogeneous throughout the basin. At the FAO divisions' level, the non-linear smoothing term for year (Figure 3a–c) was significant for seven of the eight considered sectors (five with $\alpha = 0.05$ and two considering $\alpha = 0.1$) and five of these six significant trajectories ended in recent declines (Figure 3b). These declines began earlier and were more intense in the peripheral sectors, such as the Marmara Sea (1961 – 96.0%, range 92%–100%), Adriatic Sea (1883 – 94.1%, range 90%–100%) and the Balearic (1954 – 82.5%, range 76%–98%) than central Mediterranean sectors (Ionian from 1988 a 52.1% decline, range 37%–88%; and Sardinia from 1980 a 76.4% decline, range 75%–91%).

3.2.2 | Spatial patterns and distribution shrinkage

Our standardized indices of shark abundance identified heterogeneous spatial distribution landscapes. The main hot spots were located in the western Mediterranean sectors (Figure 2b), especially in the Balearic Islands (0.73, CI 0.51–1.05), Maltese waters (0.37, CI 0.21–0.64) and Corsica (0.34, CI 0.18–0.65). Shark abundance cold spots were in all Eastern Mediterranean GSAs, except for the Marmara and Aegean Sea. When we aggregated the records in two time bins (1945–1980; 1980–2016), we detected a significant contraction of the species' spatial distribution. All the Mediterranean Sea peripheral sectors recorded a decrease in shark abundance in the second period (Figure 4c), with the highest difference detected in the Marmara Sea (−96.6%, CI −95.2% to −<99.9%), followed by the Balearic (−73.1%, CI −72.5% to −74.7%) and the Gulf of Lions (−38.0%, CI −41.4% to −18.3%). All the central sectors, instead, highlighted an increase in the shark abundance (Figure 4c), with the highest value detected in the Ionian division (+222.6%, CI +191.6% to +322.4%).

4 | DISCUSSION

Conservation actions and recovery plans for threatened and endangered marine top predators are broadly limited by a lack of information on the population status and trends at the scale of whole ecoregions and over multi-decadal time scales. By analysing 156 years of white shark records in the Mediterranean Sea, we were able, for the first time, to estimate large-scale and long-term trajectories of white shark abundance indices across the entire region. The use of all the available sources of information, integrated with a proxy controlling for the observation effort change within space and time, permitted us to standardize our trends. These standardized indices of population abundance suggested that the species went through a complex trajectory of change, characterized by an increasing phase followed by a sharp decline since the 1980s. The recent decline, together with a detected range contraction in the spatial distribution of records (Worm & Tittensor, 2011), and stronger and more prolonged declines estimated in peripheral regions compared to central sectors, suggest an overall rapid decline of the white shark population in the region in the last 3–4 decades. Our results are in contrast with population abundance increases inferred in other regions, such as California (Lowe et al., 2012), north-western Atlantic (Curtis et al., 2014), South Africa (Dudley & Simpfendorfer, 2006) and Australia (Reid et al., 2011). Conversely, they are in line with regions where the white shark occurrence data are sparse and infrequent, such as the Northwest Pacific Ocean (Christiansen et al., 2014). These results confirmed earlier evidence of regional declines provided by McPherson and Myers (2009), Boldrocchi et al., (2017) and Ferretti et al. (2008) for a larger taxonomic group, but scaled-down recent Red List assessments carried out by the IUCN, which classified the white shark as critically endangered in the Mediterranean Sea and European waters (Dulvy et al., 2016; Nieto et al., 2015). Our results suggest instead an overall decline of 61.5% over the last 10 years or three generations, which would classify the species as endangered (EN) "if the reduction causes may not have ceased or well understood," as stated in IUCN Criteria Version 3.1 (A2-bc). Taken together, our results and those of studies conducted elsewhere highlight the importance of regional analyses and the risk of extrapolating trends across different geographies. It is easily perceivable that each region has peculiar characteristics, history of human impact and drivers of change. An informative regional assessment would prevent wastage of both conservation efforts and resources.

Similarly, we confirmed previous evidence of the prevalence of Mediterranean white sharks in western sectors (Boldrocchi et al., 2017), characterized by distinct bioecological and physical oceanographic characteristics from the Eastern Mediterranean. The west–east temperature (Bosc, Bricaud, & Antoine, 2004) and productivity (Coll et al., 2010) gradients would make the warmer Eastern Mediterranean waters a suboptimal habitat for adult endothermic white sharks (Carey et al., 1982). By contrast, the colder and productive western sectors could represent resource hot spots for the species. These are in fact important breeding and feeding ground for bluefin tunas (Cermeño et al., 2015) and small cetaceans (Gnone et al., 2011; Lauriano, Pierantonio, Donovan, & Panigada, 2014), which are important food items for the white sharks (Figure 1d, Boldrocchi et al., 2017). This result highlights

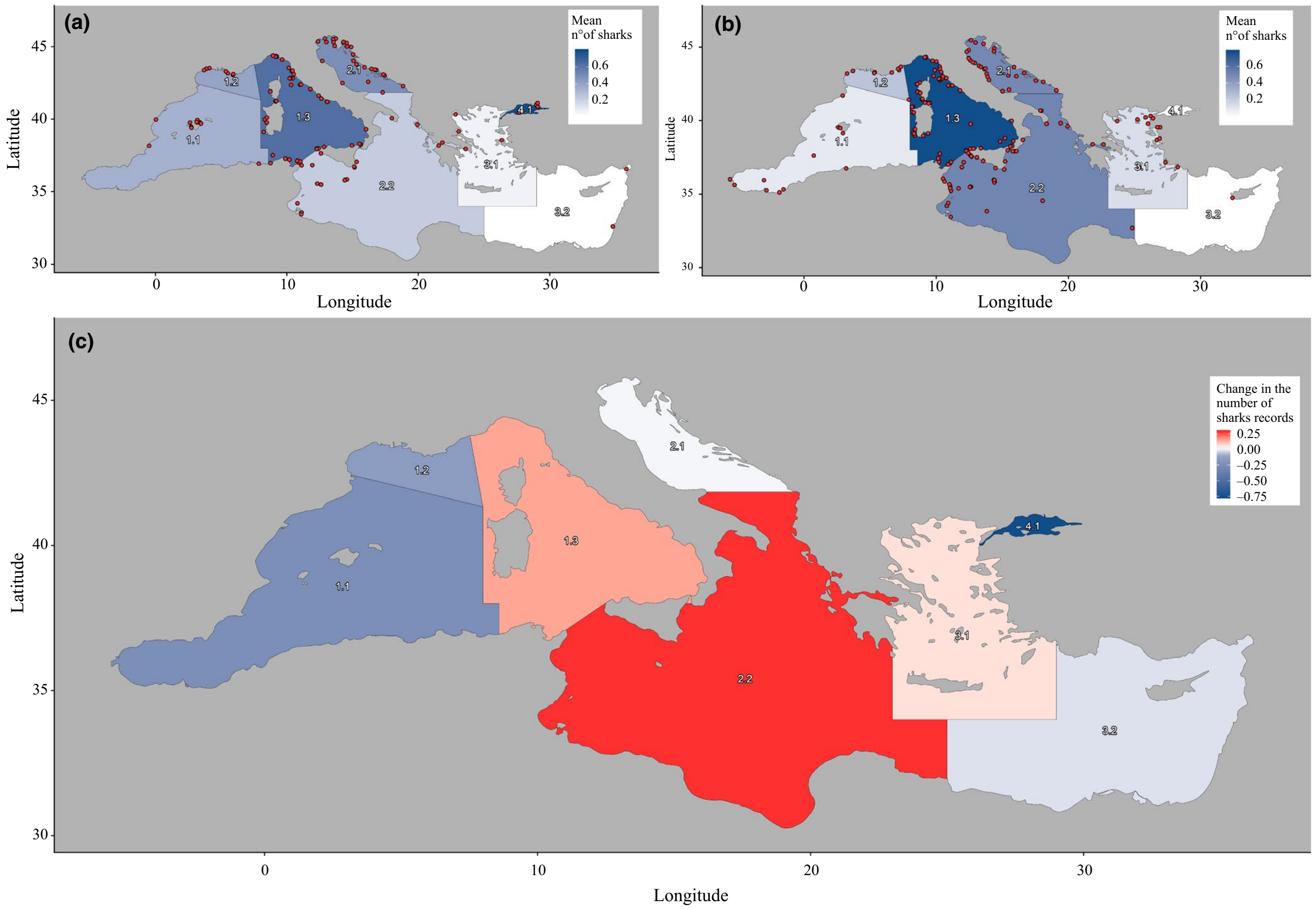

FIGURE 4 Spatial range contraction. Predicted mean annual no. of sharks every five million people for each FAO division in time intervals: (a) 1945–1975, (b) 1976–2016. The red dots in the maps show the white sharks sighting locations in each period. (c) Variation between 1945–1975 and 1976–2016 time bins. Red sectors correspond to abundance rise, while blue sectors correspond to abundance decline

the critical importance of the western sectors for the persistence of white shark populations.

The white shark ecology in the Mediterranean Sea is still poorly characterized and these analyses are a step forward addressing this important issue. Among the multiple hypotheses that may explain the estimated trajectories of change, we highlight three potential drivers. First, over the last 200 years, coastal fishing in the Mediterranean Sea has notably increased and expanded throughout the region (Piroddi et al., 2015) impacting both juvenile and adult white sharks, but contemporarily increasing the number of occurrence records. Young-of-the-year and juvenile white sharks are vulnerable to inshore gears such as trammel or gill nets (Bruce & Bradford, 2012; Curtis et al., 2014; Lowe et al., 2012), which have been massively used all along the Mediterranean shores also for targeting sharks (Ferretti, Osio, Jenkins, Rosenberg, & Lotze, 2013). Adult individuals were frequently reported in tuna traps (>50% of catches on record, Figure 1e), which were fixed gears historically used to catch bluefin tunas on their migratory routes in the Mediterranean Sea (Bombace & Lucchetti, 2011) and could have represented a source of mortality for white sharks for centuries. Since the 1960s, tuna traps ceased to be profitable and most have been closed as an effect of tuna overexploitation by industrial purse seining and other pelagic fisheries (Fromentin & Powers, 2005; ICCAT, 2017; Rouyer et al., 2018). This may have reduced the impact on adult white sharks as well as the number of catches we had on record. Meanwhile, white sharks began to be exposed to offshore fishing, especially tuna and swordfish longlining, which greatly escalated in the region during the last 50 years (Ferretti et al., 2008). In this period, white sharks were exposed to both inshore and offshore fishing and could not benefit from sheltering offshore which was practically unexploited historically (Ferretti et al., 2008). Similar patterns have been observed in South Africa and Australia (Dudley & Simpfendorfer, 2006; Ferretti et al., 2010; Reid et al., 2011).

It is also possible that Mediterranean white sharks have followed the population trajectory of Bluefin tuna, one of their most frequent prey in the region (Boldrocchi et al., 2017; De Maddalena & Heim, 2012; Kabasakal, 2016). In our data, 27.3% of the white sharks with stomach content data ate bony fish and 47% of these fishes were tunas (Figure 1d, Table S6). Tunas are suitable prey for white sharks (Hussey et al., 2012) and the bluefin tuna's overexploitation in the last 50 years may have reduced one of the most important prey resources for this species in the area (ICCAT, 2017; Rouyer et al., 2018). The long-term trajectory we estimated for the white shark records has a temporal phase similar to the time series of Mediterranean bluefin tuna abundance estimated from centuries of tuna trap data (Ravier & Fromentin, 2001). The bluefin tuna decline detected in recent decades (Fromentin & Powers, 2005; Rouyer et al., 2018) coincides with the recent decline of the white shark sighting rate, supporting the plausibility of a predator–prey dynamic between the two species. Yet tuna overexploitation also caused the end of the tuna trap fishery. Therefore, it is unclear whether such a contemporary decline in sighting rate has been caused by the end of an important source of white shark mortality in the region (i.e. decline in catch records from tuna traps), or by an underlining population decline through indirect bottom-up effects (because of the decline of an important prey), or both factors combined. However, no differences in GAM's trajectories were detected by fitting the FAO model with and without the tuna trap catches (Supporting Information, Figure S9) in all sectors but the Balearic (Division 1.1), a piece of evidence against the decline in catch record hypothesis. Whereas, the predator–prey hypothesis is corroborated by the fact that adult white sharks' preferential prey, such as pinnipeds and whale carcasses (Hussey et al., 2012), have been much scarcer or essentially absent in the Mediterranean Sea for most of the period considered in this analysis. The only pinniped in the region, the monk seal (*Monachus monachus*, Phocidae), has small remnant populations only in the Eastern Mediterranean sectors (Karamanlidis & Dendrinos, 2015) and was considered rare (heavily depleted by centuries of overhunting) in most of the Mediterranean Sea by the 18th century (Johnson, 2004). Whale abundance is also much lower than in other ocean sectors where white sharks occur (Notarbartolo di Sciara, 2002). It is, therefore, possible that adult white sharks adapted to feed mainly on tunas in the Mediterranean Sea; a hypothesis that would make this population unique respect other global populations and should be formally tested in future research.

The above explanations are confounded by the change in observation effort expected from the spatial and temporal expansions of fisheries and other factors affecting the probability to detect records. We used trajectories of human population change along the Mediterranean coasts as a single and practical proxy of observation effort, but human population abundance is one of its multiple components. For example, linguistic barriers and political instability may have limited the number of records we found in North African and Middle Eastern regions, as well as the two World Wars and the 1918 Flu Pandemic may have acted similarly in Europe during these periods (D'Ancona, 1949; Thurstan, Brockington, & Roberts, 2010). In addition, episodic events, such as a 19th-century reward programme issued by the Imperial Maritime Austrian Government to cull white sharks in the Adriatic Sea (De Marchesetti, 1882), could have boosted the probability to have occurrence records independent of human population changes. Similarly, the expansion of the use of the Internet and social networks in the last 20 years has likely increased the probability that a record of a white shark capture is reported. International (CITES, CSM, Barcelona and Bern Conventions) and national legislation (in Malta, Israel, Croatia, Montenegro and Slovenia) to protect this species may have deterred Mediterranean fishermen in reporting catches, fearing disruptive or legal consequences for their activities. Although these factors may have acted in different direction (i.e. biasing upward or downward the estimated trends), the probabilistic distribution we used to handle the response variable allows clustered observations, quantifying these sources of bias is now a top priority to further explaining and reducing uncertainty of the general large-scale spatial and temporal patterns we identified. Nevertheless, our modelling approach represents an innovation in analysing opportunistic data, by testing observation effort regimes that are not simulated, as done so far (Christiansen et al., 2014; Curtis et al., 2014; McPherson & Myers, 2009), but quantitatively estimated through the use of a proper observation effort proxy. Indeed, most of the cited features affecting observation effort are in some ways related to demographical changes of the human population (i.e. fishing pressure, technological development). Hence, adopting an observation effort proportional to the human population mitigates the confusing effects of the mentioned factors.

Reconstruction of the Mediterranean white shark spatio-temporal patterns of abundance, obtained by using all available occurrence records, generated new hypotheses on the species' population structure and predator–prey dynamics in the region. Testing these hypotheses with further dedicated research will further contribute to reconstruct population baselines of this species and deepen our understanding of its life history, ecology and biogeography. These aspects are crucial to ensure the conservation of white sharks in the region and across the planet. We also identified occurrence hot spots that would represent important sampling locations for collecting high-quality biological data, including tracking data to directly assess distribution, foraging and habitat use. These field studies are expensive and require careful planning on where and when white sharks are most likely detected.

Globally, there are multiple species of conservation concern with a similar scantiness of abundance data that would benefit from our approach of combining all available occurrence data. Our study shows that a careful examination of these data, even if opportunistic, can reveal important ecological patterns, particularly regarding trends in abundance and spatial distribution, that are critical to inform adequate conservation actions and science-based recovery plans.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding and senior authors (stefano.moro@uniroma1.it and ferretti@vt.edu) upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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